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SEED-COAT COLOR GENES IN SIX COMMERCIAL VARIETIES OF BEANS[1]

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INTRODUCTION

WHITE SEED in beans results from two main genetic causes: (1) the beans may lack the primary pigmentation factor, first called P by Shull (1907);[3] or (2) they may, according to Lamprecht (1932*a*, *b*; 1933; 1936; 1939), have the P gene, but still be white because no dominant seed-color genes are present.

Beans in the first group may carry any number of dominant seed-coat color genes which cannot be expressed in the presence of p. When this type of white bean is crossed to a colored bean, the first generation is colored and the F_2 generation segregates 3 colored: 1 white.

When beans of the second type are crossed to colored, the F_1 is colored and the F_2 segregation of colored and white is 3:1, 15:1, 63:1, or 255:1, depending on whether 1, 2, 3, or 4 independent color genes were in the colored parent. The numerous seed-coat colors result from the interaction of the dominant color genes. According to this hypothesis, each dominant color gene with P will impart a definite color to the seed coat. The recessive allele of any color gene then cannot cause color. For this reason, Lamprecht (1947) has refused to accept the Rk gene worked on in this laboratory (Smith, 1939; 1947) because the dominant Rk is buff and the recessive rk is testaceous (brick red). A third allele, rk^d, which causes a garnet brown (dark red) seed-coat color, has been described (Smith and Madsen, 1948). Of the Rk gene, Lamprecht (1947) wrote: "... as is evident, the cross-results published by Smith give no proof for the existence of a gene Rk which in its recessive state causes red coloring of the testa. Instead of this the apparently recessive segregation of red colors was caused by a segregation in other color genes, which in their dominant state govern the red seed-coat color. Thus the symbol Rk for a gene causing a recessive red testa should be deleted from the literature." In order to study this problem further, seed of a P-white line of beans was obtained from Lamprecht. He sent Line 214, a sister strain to Line 146 which was used as a tester line in

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[3] See "Literature Cited" for citations referred to in the text by author and date.

crosses he reported in 1936. Hybrids between this tester and colored varieties should give critical information on the controversy on the Rk gene. According to Lamprecht, Line 214 has the genetic constitution P c j g b ins v r.

MATERIALS AND METHODS

Pollen from Line 214 was used to make hybrids with six commercial varieties of dry beans: Pinto, Bayo, Pink, Michigan Dark Red Kidney, Great Northern, and Small White. The colors of the F_1 hybrids are reported under "Results." The number of plants in the F_2 are not reported because some errors were made in the color classifications, and were not straightened out until the F_3 results were obtained. This report is based on the genotype analyses of the various colors obtained by growing progenies from F_2 plants. A single seed from each F_3 plant was harvested, and the seed from each progeny row was stored in an envelope. These beans were later classified for color, and the number of plants of each color in each progeny was recorded.

RESULTS

A scheme of inheritance was developed which would explain the results of the F_2 progenies of each cross that would be consistent with the results of the other crosses. This necessitated an hypothesis assuming the interaction of six genes, as follows:

1. P, the primary pigmentation gene named by Shull (1907). In the present study, the four colored varieties and Line 214 had P, and the two white varieties had p.

2. M, the mottling gene named by Shull (1907). It was later found by Lamprecht (1947) to be an allele of the R gene, to which he gave the symbol R^{ma}. M behaves as a dominant that segregates 3 mottled:1 self-colored. The colors of both the mottled areas and the background are determined by other seed-coat color genes. M was present in three of the six varieties tested—Pinto, Bayo, and Great Northern.

3. Rk, a color gene described by the author (1939; 1947; Smith and Madsen, 1948). This gene produces a pinkish-buff seed coat. There are three alleles of the Rk gene: Rk (buff); rk (testaceous or pink); and rk^d (dark red). Three of the six varieties are known to have the buff gene Rk—Pinto, Bayo, and Great Northern—while Pink has rk, and Dark Red Kidney has rk^d. The breeding results of crosses with Line 214 indicate that it carried Rk. Beans of the constitution of P Rk and P rk are both white if accompanied by no other color genes. All the tested varieties have G in addition to P.

4. Br, a brown modifier reported earlier from this laboratory (Smith, 1947). The difference between Pinto (brown/buff) and Bayo (green/buff) is due to the presence of Br in Pinto and br in Bayo. Since none of Lamprecht's genes seems to approximate this gene, the Br gene nomenclature is retained in this report.

5. G, described by Lamprecht (1932*a*). Beans of the constitution P G are faintly yellow with a brown hilum ring. The G symbol is used in this report

because it is necessary to assume a brown modifier in addition to Br, to explain the results.

6. B, described by Lamprecht (1932*a*). The combination P B was described as having a pale violet-white color that is often distributed in minute dots over the seed coat, accompanied by a yellow-brown hilum ring. In the present study this color is called gray-white. The B gene seems more appropriate to describe the results of these studies than does Lamprecht's (1936) gray-white, Gri, because the prominent hilum ring encountered here better resembles Lamprecht's B gene than the Gri which has no hilum ring. Furthermore, beans of the constitution P c Gri were assumed by Lamprecht to be pure white. This result was not obtained in the present study.

Another gene was probably present in the Pinto and Great Northern crosses. The F_1 of both of these was double-mottled, brown/drab/buff, and all the double-mottled F_2 plants segregated double-mottled and single-mottled types, while the single-mottled beans did not segregate double-mottled. In the Pinto cross, F_3 progenies from 24 double-mottled F_2 plants were grown. They segregated 318 double-mottled:208 single-mottled. In the Great Northern cross, 12 double-mottled F_2 plants segregated 93 double-mottled:99 single-mottled in F_3. At first it was thought that the double mottling might be due to the C gene (Lamprecht, 1932*a*, *b*) which, when heterozygous, gives mottling. The results of the two crosses are too divergent for such an explanation. Double mottling was apparent in only one mottled type—those beans with M Rk Br G B. If Cc was the cause of double mottling, the corresponding CC and cc types were not distinguishable. The cause of the double mottling was left unsolved, and the report of the results does not distinguish double-mottled brown/drab/buff from single-mottled drab/buff.

The proposed genetic constitutions of the six varieties studied, with the genes segregating in each cross and the color of the F_1 plants, are as follows:

		F_1 GENOTYPES	COLOR OF F_1 PLANTS
Pinto:	P M Rk Br G B	P M/m Rk Br/br G/b B/b	Brown/drab/buff
Great Northern:	p M Rk Br G B	P/p M/m Rk Br/br G/g B/b	Brown/drab/buff
Bayo:	P M Rk br G B	P M/m Rk Br/br G/g B/b	Green/buff
Sutter Pink:	P m rk br G B	P m Rk/rk br G/g B/b	Buff
Michigan Dark Red Kidney:	P m rk^d br G b	P m Rk/rk^d Br/br G/g b	Drab
Small White:	p m Rk Br G B	P/p m Rk Br/br G/g B/b	Drab

Table 1 lists the proposed genetic formulas for the colors obtained in F_2 populations and shows the color segregants that appeared in the F_2 hybrids on each variety. The latter are marked with an X in the appropriate places. In some cases the same color may be caused by more than one genotype. If more than one recognizable genotype in a given phenotype was encountered, the place in question is designated with an asterisk.

Families from each of the color types found in the F_2 were tested in F_3 to obtain the genotypes of the F_2 plants. In reporting the progeny tests, the proposed F_2 genotypes and the colors obtained in F_3 are listed.

TABLE 1

GENETIC CONSTITUTION OF SEED-COAT COLORS FOUND IN SIX CROSSES WITH LINE 214

Genetic constitution	Color	Found in F_2 progenies of crosses with:					
		Pinto	Gt. N.	Bayo	Pink	D.R.K.	Sm. W.
P M Rk Br G B....	Drab/buff	×	×	..	..	..	..
P M Rk Br G b....	———	..	*	..	..	..	..
P M Rk Br g B....	Drab/gray-white	×	×	..	..	..	..
P M Rk Br g b....	Drab/white	×	×	..	..	..	..
P M Rk br G B....	Green/buff	×	×	×	..	..	..
P M Rk br G b....	———	*	*	*	..	..	..
P M Rk br g B....	Green/gray-white	×	×	×	..	..	..
P M Rk br g b....	Green/white	×	×	×	..	..	..
P m Rk Br G B....	Drab	×	×	..	..	..	×
P m Rk Br G b....	———	*	*	..	..	×	..
P m Rk br G B....	Buff	×	×	×	×	..	×
P m Rk br G b....	———	*	*	*	*	×	..
P m rk br G B....	Pink	..	..	..	×	..	..
P m rk br G b....	———	..	..	..	*	..	..
P m rk^d Br G b....	Liver brown	..	..	..	..	×	..
P m rk^d br G b....	Garnet brown	..	..	..	..	×	..
P m Rk Br g B....	Gray-white	×	×	..	..	..	×
P m Rk br g B....	———	*	*	×	×	..	*
P m rk Br g B....	———	..	..	..	..	..	..
P m rk br g B....	———	..	..	..	*	..	..
P m Rk Br g b....	White	×	×	..	..	×	..
P m Rk br g b....	———	*	*	×	×	*	×
P m rk Br g b....	———	..	..	..	*	..	..
P m rk br g b....	———	..	..	..	..	..	..
p-----....	White	..	×	..	..	..	×

* = more than one recognizable genotype in a given phenotype.

Pinto × Line 214

The F_2 genotypes and the segregation products of the different colors are listed in table 2.

Four segregating genes were found in this cross. Ninety-six F_2 progenies were grown in F_3. The total number of plants in populations segregating for each of these genes was as follows:

838 M : 264 m	P = .10 – .05
481 Br : 156 br	.80 – .70
1,606 G : 611 g	.01
708 B : 250 b	.50 – .30

Drab/buff, M Br G B. Twenty-nine F_2 lines of this color were tested in F_3. The genetic composition of the lines is shown in table 2. In the families segregating for four genes, 10 color types were found. In those in which Br was homozygous, no green/buff, green/gray-white, green/white, or buff segregants were obtained because each of those colors is expressed only in the presence of br. In those families in which B was homozygous, no drab/white, green/white, or white was expected because b must be present for their expression. When M was homozygous, no self-colored types were found. The presence of homozygous G prevented the appear-

TABLE 2

F_2 GENOTYPES TESTED IN PINTO × LINE 214

F_2 color and no. progenies tested	No. of seg. genes	No. of F_3 families	F_2 genotypes	Colors in F_3									
				Drab/buff M Br G –	Drab/gray-white M Br g B	Drab/white M Br g b	Green/buff M br G –	Green/gray-white M br g B	Green/white M br g b	Drab m Br G –	Buff m br G –	Gray-white m – g B	White m – g b
Drab/buff (29)	4	9	M/m Br/br G/g B/b	X	X	X	X	X	X	X	X	X	X
	3	6	M/m Br G/g B/b	X	X	X	..	..	..	X	..	X	X
	3	1	M/m Br/br G/g B	X	X	..	X	X	..	X	X	X	..
	3	1	M Br/br G/g B/b	X	X	X	X	X	X	..	..	..	..
	2	5	M/m Br/br G B	X	..	..	X	..	..	X	X	..	..
	2	1	M/m Br G/g B	X	X	..	..	..	..	X	..	X	..
	2	1	M Br/br G/g B	X	X	..	X	X	..	..	..	..	..
	1	3	M/m Br G B	X	..	..	..	..	..	X	..	..	..
	1	1	M Br G/g B	X	X	..	..	..	..	..	..	..	..
	0	1	M Br G B	X	..	..	..	..	..	..	..	..	..
Drab/gray-white (3)	3	2	M/m Br/br g B/b	..	X	X	..	X	X	..	..	X	X
	2	1	M Br/br g B/b	..	X	X	..	X	X	..	..	..	..
Drab/white (3)	2	2	M/m Br/br g b	..	..	X	..	..	X	..	..	..	X
	1	1	M Br/br g b	..	..	X	..	..	X	..	..	..	..
Green/buff (9)	3	6	M/m br G/g B/b	..	..	..	X	X	X	..	X	X	X
	2	1	M/m br G/g B	..	..	..	X	X	..	..	X	X	..
	1	2	M br G/g B	..	..	..	X	X	..	..	..	..	..
Green/gray-white (6)	2	3	M/m br g B/b	..	..	..	..	X	X	..	..	X	X
	1	1	M br g B/b	..	..	..	..	X	X	..	..	..	..
	1	1	M/m br g B	..	..	..	..	X	..	..	..	X	..
	0	1	M br g B	..	..	..	..	X	..	..	..	..	..
Green/white (3)	1	3	M/m br g b	..	..	..	..	..	X	..	..	..	X
Drab (19)	3	3	m Br/br G/g B/b	..	..	..	..	..	..	X	X	X	X
	2	3	m Br/br G/g B	..	..	..	..	..	..	X	X	X	..
	2	5	m Br/br G/g b	..	..	..	..	..	..	X	X	..	X
	2	1	m Br G/g B/b	..	..	..	..	..	..	X	..	X	X
	1	1	m Br/br G B	..	..	..	..	..	..	X	X	..	..
	1	2	m Br G/g B	..	..	..	..	..	..	X	..	X	..
	1	4	m Br G/g b	..	..	..	..	..	..	X	..	..	X
Buff (8)	2	2	m br G/g B/b	..	..	..	..	..	..	..	X	X	X
	1	1	m br G/g B	..	..	..	..	..	..	..	X	X	..
	1	2	m br G/g b	..	..	..	..	..	..	..	X	..	X
	0	3	m br G –	..	..	..	..	..	..	..	X	..	..
Gray-white (13)	1	10	m – g B/b	..	..	..	..	..	..	..	..	X	X
	0	3	m – g B	..	..	..	..	..	..	..	..	X	..
White (3)	0	3	m – g b	..	..	..	..	..	..	..	..	..	X

ance of either mottled or self-colored gray-white or white types, either in mottled or self-colored beans. The other segregating populations were amply accounted for by the interaction of different combinations of homozygous dominant genes.

Drab/gray-white, M Br g B. In this genetic combination, all colors requiring the presence of G do not appear in the F_3 population. Only three F_2 progenies were tested, in which two genotypes were found, one segregating for all three genes and one segregating for Br and B.

Drab/white, M Br g b. This color can segregate only for M and Br. In the three progenies tested, two genotypes were found, one segregating for both, the other for Br only.

Green/buff, M br G B or M br G b. Since B shows no effect on this color, it may be present in either the dominant or recessive form. The segregation products disclose whether B or b was present. In nine progeny tests, three genotypes were found: segregating for M, G, and B; segregating for M and G; and segregating for G only. The latter two were homozygous for B because no whites appeared in their progeny.

Green/gray-white, M br g B. Six progenies were tested, disclosing four genotypes: those segregating for both M and B; those segregating for M only; those segregating for B only; and those segregating for neither.

Green/white, M br g b. This color can segregate only for the mottling gene, M. All three progenies tested segregated.

Drab, m Br G B or m Br G b. The drab color is due to the interaction of Rk, Br, and G in the presence of m. Furthermore, drab beans may have either B or b. The buff color is due to the Rk gene with G and br. Gray-white may have either Br or br so long as g and B are present, and white may have Br or br so long as g and b are present. Drab beans segregating for three genes would have drab, buff, gray-white, and white progeny. Those segregating for Br and G with B homozygous would have no white progeny, and those segregating for the same genes with b would produce no gray-white progeny. Plants with drab seed which are homozygous for Br but segregating for G would produce no buff seed.

Thus, drab could segregate monohybrid ratios for drab and buff, drab and gray-white, or drab and white. Since both parents contributed Rk, some of the whites must have had both Rk and Br. The brown modifier, Br, has not shown the ability to produce a color by itself, but the Rk gene has been shown repeatedly to be a seed-coat color producing gene.

Buff, m br G B or m br G b. Eight F_2 progenies were tested. Segregation was obtained for both G and B. Other F_2 plants were segregating for G only. Two F_2 plants had B, and one had b. Buff therefore depends on a particular combination, P m br G.

Gray-white, m–g B. This color can segregate only for B. The symbol for Br is left blank because gray-white may have either Br or br. Of 13 progenies tested, 10 segregated and three bred true.

White, m–g B. This color must breed true. The three tested did so.

Some of the whites from drab F_2 plants must have had Br. Since both parents contributed Rk, these whites must have had both Br and Rk. The

F_2 GENOTYPES TESTED IN GREAT NORTHERN × LINE 214

F_2 color and no. progenies tested	No. of segregenes	No. of F_3 families	F_2 genotypes	Colors in F_3: Drab/buff M Br G –	Drab/gray-white M Br g B	Drab/white M Br g b	Green/buff M br G –	Green/gray-white M br g B	Green/white M br g b	Drab m Br G –	Buff m br G –	Gray-white m – g B	White m – g b
Drab/buff (18)	5	8	P/p M/m Br/br G/g B/b	×	×	×	×	×	×	×	×	×	67/256
	4	1	P/p M/m Br G/g B/b	×	×	×	×	×	×	×	.	×	67/256
	4	2	P/p M Br/br G/g B/b	×	×	×	×	×	×	×	.	.	1/4
	3	2	P/p M/m Br/br G B	×	×	×	×	.	.	×	×	.	1/4
	3	1	P M/m Br G/g B/b	×	×	×	×	.	.	×	.	.	1/4
	2	1	P/p M Br/br G B	×	×	×	.	.	.	.	.	×	1/64
	2	1	P/p M Br G/g b	×	×	×	×	×	.	.	.	.	1/4
	2	1	P M/m Br G/g b	×	×	×	.	.	.	.	.	.	1/4
	1	1	P M Br G/g B	×	.	×	.	.	.	×	.	.	1/16
Drab/gray-white (10)	4	2	P/p M/m Br/br g B/b	.	×	×	.	.	.	.	.	.	....
	3	1	P M/m Br/br g B/b	.	×	×	.	×	×	.	.	×	76/256
	3	2	P/p M/m Br/br g B	.	×	.	.	×	×	.	.	×	1/16
	3	1	P/p M/m Br g B/b	.	×	×	.	×	.	.	.	×	1/4
	2	1	P M/m Br g B/b	.	×	×	.	.	.	.	.	×	19/64
	2	1	P/p M/m Br g B	.	×	.	.	.	.	.	.	×	1/16
	1	1	P M/m Br g B	.	×	.	.	.	.	.	.	×	1/4
	1	1	P/p M Br g B	.	.	.	.	.	.	.	.	.	....
Drab/white (1)	1	1	P/p M Br g b	.	.	×	.	.	.	.	.	.	1/4
Green/buff (18)	4	3	P/p M/m br G/g B/b	.	.	.	×	×	×	.	×	×	67/256
	3	2	P M/m br G/g B/b	.	.	.	×	×	×	.	×	×	1/64
	3	1	P/p M br G/g B/b	.	.	.	×	×	×	.	.	.	1/4
	2	1	P/p M br G/g B	.	.	.	×	×	.	.	.	.	1/4
	2	4	P/p M br G/g b	.	.	.	×	×	.	.	.	.	1/4
	2	1	P/p M/m br G B	.	.	.	×	.	×	.	.	.	1/4
	2	4	P M/m br G/g B	.	.	.	×	.	.	.	×	.	1/4
	1	1	P/p M br G B	.	.	.	×	×	.	.	×	×	....
	1	1	P M/m br G B	.	.	.	×	.	.	.	×	.	1/4
Drab (11)	4	1	P/p m Br/br G/g B/b	.	.	.	.	.	.	×	×	×	....
	3	2	P m Br/br G/g B/b	.	.	.	.	.	.	×	×	×	19/64
	2	1	P/p m Br/br G B	.	.	.	.	.	.	×	×	×	1/16
	2	1	P/p m Br G/g b	.	.	.	.	.	.	×	×	.	1/4
	1	2	P m Br/br G B	.	.	.	.	.	.	×	×	.	7/16
	1	4	P/p m Br G B	.	.	.	.	.	.	×	×	.	....
Buff (2)	1	1	P m br G/g B	.	.	.	.	.	.	.	.	.	1/4
	1	1	P/p m br G B *or* P m br G/g b	.	.	.	.	.	.	.	×	×	....
				.	.	.	.	.	.	.	×	.	1/4
Gray-white (7)	2	3	P/p m – g B/b	.	.	.	.	.	.	.	.	×	....
	1	4	P/p m – g B *or* P m – g B/b	.	.	.	.	.	.	.	.	×	7/16
				.	.	.	.	.	.	.	.	×	1/4

results of this cross indicate that P-white beans may carry the dominant color modifier, Br, and the dominant Rk gene. In former studies in this laboratory, the G gene was present in both parents of the crosses. The dominant Rk appears much like Lamprecht's (1939) description of his J gene. However, since his tests indicate that Line 214 carried the recessive j, Rk must be a different gene. The fact that beans with the constitution of P m Br Rk g b are white indicates that the hypothesis that P-white beans contain no dominant genes for color is not entirely true—unless the hypothesis is broadened a little. P Rk beans are not buff unless G is present. If the assumption is made that Rk is a modifier of G, rather than a primary color-producer, the results can be explained by the Lamprecht scheme of color reactions.

Great Northern × Line 214

The white-seeded Great Northern variety has been shown to have the same seed-coat color genes as Pinto (Smith and Madsen, 1948). As expected, the breeding behavior of the different color types was the same as in the Pinto cross except that the P gene was segregating. The color of the F_1 plants was similar, and the same colors were obtained in the F_2 generation. In this cross, five genes were segregating. Where it was possible to distinguish the dominant and recessive genes in segregating F_3 families the results for each gene were as follows:

511 P : 170 p	P = .95
281 M : 65 m	.01
524 Br : 167 br	.80 – .70
777 G : 232 g	.20 – .10
133 B : 87 b	.001

Most of the deviations in the segregation of B occurred in the progeny from drab/buff F_2 plants. If these are eliminated, the ratio of B/b is 110:43, with a P value between .50 and .30. The results of the genotype analyses of the F_2 plants of this cross are shown in table 3.

The same colors were obtained in this cross as in the Pinto hybrids. In F_2 progeny tests, those which segregated for P produced one fourth p white plants. Some genotypes also segregated P-white progeny. In the mottled F_2 plant progeny, the presence of P white is indicated by the appearance of mottled beans with a white background. The P-white and p-white cannot be distinguished when m is present, but there is an excess of whites over one fourth of the population. In case drab/buff was segregating for P, M, Br, G, and B or for P, M, G, and B, P whites would increase the expected ratio of whites by 3/256, or a total of 67/256, while only 1/64 white is expected if P is not segregating but M, G, and B are. A number of genotypes were found which segregated for P but not for B, so that a 3:1 ratio of colored and white was obtained. In the drab/gray-white progenies, the first two listed in table 3 differ only in the proportion of whites obtained. The first one listed segregated for P, M, Br, and B, in which 76/256 of the population was white, while in the next line, the genotype segregating for M, Br, and B, only 1/16 was white.

TABLE 4

F_2 GENOTYPES TESTED IN BAYO × LINE 214

F_2 color and no. progenies tested	No. of seg. genes	No. of F_3 families	F_2 genotypes	Colors in F_3					
				Green/buff M br G –	Green/gray-white M br g B	Green/white M br g b	Buff m br G –	Gray-white m br g B	White m br g b
Green/buff (26)	3	5	M/m G/g B/b	×	×	×	×	×	×
	2	5	M/m G/g B	×	×	..	×	×	..
	2	6	M/m G/g b	×	..	×	×	..	×
	1	6	M/m G B	×	..	..	×	..	..
	1	1	M G/g B	×	×	..	..	..	..
	1	3	M G/g b	×	..	×	..	..	..
Green/gray-white (5)	2	1	M/m g B/b	..	×	×	..	×	×
	1	2	M g B/b	..	×	×	..	..	..
	1	1	M/m g B	..	×	..	..	×	..
	0	1	M g B	..	×	..	..	..	..
Green/white (4)	1	4	M/m g b	..	..	×	..	..	×
Buff (10)	2	3	m G/g B/b	..	..	..	×	×	×
	1	6	m G/g B	..	..	..	×	×	..
	0	1	m G B	..	..	..	×	..	..
Gray-white (4)	1	2	m g B/b	..	..	..	..	×	×
	0	2	m g B	..	..	..	..	×	..

The gray-white, P m br g B, had three F_3 families segregating for both P and B, giving a 9:7 ratio, while four families segregated for a single gene, or a 3:1 ratio. The results for the genotypes tested in this cross are similar to those for the Pinto in all the colors tested except for the segregation of P.

Bayo × Line 214

Bayo has been shown to have the M, Rk, and br genes (Smith, 1947). The genotypes of the tested F_2 plants are shown in table 4. Both parents contributed P, br, and Rk. Therefore segregation for three genes was found. In the F_3 progenies, the three segregating genes taken separately were as follows:

30 M : 8 m	P = .70 – .50
880 G : 262 g	.70 – .50
172 B : 52 b	.70 – .50

Green/buff, M br G B. This color may segregate for the three genes M, G, or B. Progeny tests of 26 F_2 plants showed six genotypes. Only three of these genotypes were found in nine green/buff F_2 plants tested in the Pinto cross.

Green/gray-white, M br g B. This color may segregate for two genes. Five F_2 plants revealed four genotypes.

TABLE 5

F_2 GENOTYPES TESTED IN SUTTER PINK × LINE 214

F_2 color and no. progenies tested	No. of seg. genes	No. of F_3 families	F_2 genotypes	Colors in F_3			
				Buff m Rk br G –	Pink m rk br G –	Gray-white m – br g B	White m – br g b
Buff (35)	3	15	Rk/rk G/g B/b	×	×	×	×
	2	5	Rk/rk G/g B	×	×	×	..
	2	5	Rk/rk G/g b	×	×	..	×
	2	2	Rk G/g B/b	×	..	×	×
	1	5	Rk/rk G B	×	×	..	..
	1	1	Rk G/g B	×	..	×	..
	1	1	Rk G/g b	×	..	..	×
	0	1	Rk G –	×	..	..	..
Pink (12)	2	4	rk G/g B/b	..	×	×	×
	1	4	rk G/g B	..	×	×	..
	0	4	rk G –	..	×	..	..
Gray-white (14)	1	9	– g B/b	..	..	×	×
	0	5	– g B	..	..	×	..
White (1)	0	1	– g b	..	..	..	×

Green/white, M br g b. Four progeny tests revealed only one genotype segregating for M.

Buff, m br G B. Ten progenies showed four genotypes, all of which had B.

Gray-white, m br g B. This color can only segregate for B. Two progenies segregated and two bred true.

The results of this cross are in harmony with tests of the same color types in the Pinto cross.

Sutter Pink × Line 214

The pink seed-coat color has been shown to be a recessive of buff due to the Rk gene (Smith, 1947). The F_1 plants of the cross between Sutter Pink and Line 214 were self-colored buff, indicating that Rk was introduced from the white Line 214. The genes that both parents had in common were P, m, and br. The hybrids could segregate for Rk, G, and B. The segregations for these three genes in the F_2 were as follows:

784 Rk : 300 rk	P = .05 – .02
1,261 G : 438 g	.50 – .30
499 B : 146 b	.20 – .10

Results of the F_2 progeny tests of this cross are shown in table 5.

Buff, Rk G B. This color, unlike the buff types in the preceding crosses, may segregate for Rk, giving buff and pink in the presence of G and either gray-white or white in the presence of g, depending on whether B or b is present. A trihybrid ratio was found in the F_2 and in 15 of the 35 F_3 populations. As in the other crosses, the presence of B or b shows no effect on

TABLE 6

F_2 GENOTYPES TESTED IN MICHIGAN DARK RED KIDNEY × LINE 214

F_2 color and no. progenies tested	No. of seg. genes	No. of F_3 families	F_2 genotypes	Colors in F_3				
				Drab Rk Br G b	Liver brown rk^d Br G b	Buff Rk br G b	Garnet brown rk^d br G b	White – – g b
Drab (41)	3	19	Rk/rk^d Br/br G/g	×	×	×	×	×
	2	7	Rk/rk^d Br G/g	×	×	..	..	×
	2	7	Rk/rk^d Br/br G	×	×	×	×	..
	1	3	Rk/rk^d Br G	×	×	..	..	..
	1	5	Rk Br/br G	×	..	×		..
Liver brown (20)	2	14	rk^d Br/br G/g	..	×	..	×	×
	1	4	rk^d Br/br G	..	×	..	×	..
	0	2	rk^d Br G	..	×	.	.	..
Buff (39)	2	20	Rk/rk^d br G/g	..	..	×	×	×
	1	7	Rk/rk^d br G	..	..	×	×	..
	1	10	Rk br G/g	..	..	×	..	×
	0	2	Rk br G	..	..	×		..
Garnet brown (14)	1	11	rk^d br G/g	..	..	..	×	×
	0	3	rk^d br G	..	..	..	×	..

the buff color. The progenies of 35 buff F_2 plants indicated that 17 were heterozygous, 11 were homozygous for B, and six were homozygous for b. One bred true, and the presence of B or b could not be told because of G.

Pink, rk G B. Twelve progeny tests of this color revealed three genotypes. Four segregated for G and B, four for G only, and four bred true.

Gray-white, –g B. This color may have either Rk or rk, as shown above. It can segregate only for B. In nine progenies, four were segregating for B and five were homozygous for B.

White, –g b. This color must breed true. The one progeny test made did so.

This cross shows the interaction of the Rk gene with G and B. G must be present for either the dominant or recessive Rk to be asserted in a seed-coat color. Neither B nor b affects either the buff or the pink color.

Michigan Dark Red Kidney × Line 214

This variety has been studied previously (Smith and Madsen, 1948). The garnet brown color was found to be recessive to buff. This gene is designated as rk^d (dark red kidney). The F_1 of this cross was purple drab, and the F_2 segregated drab, liver brown, buff, garnet brown, and white. The two parents had P, m, and b in common. No mottled or gray-white beans were found in the F_2 or F_3 generations, indicating that both parents were m, b. Three genes may segregate. The segregations of the three genes in the F_3 progenies were as follows:

977 Rk : 341 rk^d	P = .50 – .30
1,543 G : 582 g	.01
687 Br : 465 br	.001

The recessives were in excess of expectation for both G and Br. The progeny tests did not indicate any other logical explanation for the breeding behavior in the color types.

It is assumed that the Br alters the color of the Rk and rk^d phenotypes as follows: Rk Br are drab, Rk br are buff, rk^d Br are liver brown, and rk^d br are garnet brown. Br, as well as the Rk gene, must have been contributed by Line 214 in this cross. It has been shown in the other crosses that the white seed may have the following genotypes: P m Rk Br, P m Rk br (Pinto) ; P m Rk br, P m rk br (Pink) and p– – – – – (Great Northern). In the previous crosses it was assumed that Line 214 carried br. The fact that the F_1 of this cross was drab indicates that Br must have been contributed by Line 214. This leads to the assumption that Line 214 is carrying both Br and br in different plants. The F_2 genotypes of this cross are listed in table 6.

Drab, Rk Br G b. This color may segregate for three genes. Forty-one progeny tests of F_2 plants of this color revealed five genotypes. As in the other crosses, the presence of G is necessary for either allele of Rk to have effect. Since b is homozygous in this cross, the g b genotypes are white. The Br modifies Rk to drab, and the combination of Br and rk^d changes the garnet brown (dark red) to liver brown (purplish-red).

Liver brown, rk^d Br G b. This color may segregate for B and G. Four genotypes were found in 20 progeny tests. The nonappearance of drab or buff progeny indicates that rk^d was homozygous. All beans with the combination g b were white.

Buff, Rk br G b. This may segregate for Rk and G. Thirty-nine progeny tests showed four genotypes, one breeding true.

Garnet brown, rk^d br G b. This color can segregate for G only. Eleven progenies segregated and three bred true.

No whites were tested in F_3.

This cross reveals the interaction of Rk and rk^d with the brown modifier, Br, which came into the cross from the Line 214 parent.

Small White × Line 214

In this cross, as in the Great Northern cross, both parents were white. The F_1 plants were self-colored drab. It is not possible to state which parent in this cross contributed Br. Since there was no segregation for Rk, it is assumed that both parents contributed the dominant Rk. Small white must have B since gray-white appeared in the F_2 and F_3 generations. The B segregation can be followed in only two drab genotypes that were not segregating for P.

The single gene segregations in the F_3 progenies were as follows:

82 P : 38 p	P = .10 – .05
324 Br : 195 br	.001
30 B : 7 b	.50 – .30

As in the Michigan Dark Red Kidney, there was an excess of the recessive class in the Br segregations. The progeny tests made from F_2 plants are summarized in table 7.

TABLE 7

F_2 GENOTYPES TESTED IN SMALL WHITE × LINE 214

F_2 color and no. progenies tested	No. of seg. genes	No. of F_3 families	F_2 genotypes	Colors in F_3			
				Drab P Br G –	Buff P br G –	Gray-white P – g B	White P – g b **or** p – – –
Drab (32)	4	15	P/p Br/br G/g B/b	×	×	×	76/256
	3	1	P Br/br G/g B/b	×	×	×	1/16
	2	1	P Br/br G/g B	×	×	×	....
	2	5	P/p Br/br G B	×	×	..	1/4
	2	3	P Br G/g B/b	×	..	×	1/16
	1	7	P Br/br G B	×	×	..	....
Buff (16)	3	9	P/p br G/g B/b	..	×	×	19/64
	1	6	P/p – G B *or* P – G/g b	..	×	..	1/4
	0	1	P br G B	..	×	..	....
Gray-white (17)	2	7	P/p – g B/b	..	..	×	7/16
	1	8	P/p – g B *or* P – g B/b	..	..	×	1/4
	0	2	P – g B	..	..	×	....

Drab, P Br G B. This color may segregate for four genes. In 20 of the 22 drab F_2 progenies, P was segregating. As in the Great Northern cross, some genotypes segregate both P white and p white, making an excess of one fourth of the population white. Six genotypes were distinguished in the progeny tests.

Buff, P br G B. This may segregate for three genes. The same result—one fourth of the population being white—would be expected if either P or B were segregating. Sixteen progeny tests revealed three genotypes.

Gray-white, P –g B. The only segregation obtainable in this color type is white. If both P and B were segregating, 7/16 should be white. With either gene segregating alone, the ratio would be ¼ white. In the 17 progeny tests, seven segregated in a 9:7 ratio, 8 in a 3:1 ratio, and two bred true.

SUMMARY

Lamprecht's P-white Line 214 was used as a tester in crosses with six commercial varieties of beans. The genotypes of the F_2 plants were obtained by growing F_3 progenies. A consistent explanation of the breeding results requires the assumption of the interaction of six genes that determine the seed-coat colors of the varieties tested: P, M, Rk, Br, G, and B. In four of the six crosses studied there was no segregation for Rk, indicating that this dominant gene was contributed by both parents. In the two crosses in which rk or rk^d was contributed by the commercial variety, segregation for Rk was obtained. This is positive evidence that Lam-

precht's Line 214 has the dominant Rk. In the cross with Michigan Dark Red Kidney, Line 214 must have contributed the Br gene as well because the F_1 seed was drab and, in the following generations, segregation for Br was obtained.

These studies indicate that the dominant color gene G must be present for the expression of the Rk or its alleles. Thus Rk may be said to be a modifier of G just as Br is a modifier of Rk, which changes buff (Rk) to drab, and garnet brown (rk^d) to liver brown. In mottled types, Br changes green/buff to drab/buff.

Lamprecht's hypothesis that the P-white beans are free of any dominant color genes should be expanded to allow the presence of dominant color modifiers in the P-white beans.

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